

RELATIONSHIPS OF THE GENUS *HETEROCHEILA* (DIPTERA: SCIOMYZOIDEA) WITH DESCRIPTION OF A NEW FAMILY

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A morphological comparison is made of the maritime kelp-living genus *Heterocheila* Rondani with the families of Sciomyzoidea, particularly the Helcomyzidae. It is concluded that it has no particularly close relationship with any one of these families, and the new family Heterocheilidae (halfbridge flies) is established for it. *Heteromyza orientalis* Macquart, 1843 is a new synonym of *Heterocheila buccata* (Fallén, 1820).

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In the course of my recent work on the Coelopidae (kelp flies) (D. McAlpine 1991) it became apparent that (1) there is disagreement in recent literature as to the family position of *Heterocheila*, and (2) it is difficult on morphological grounds to justify the inclusion of *Heterocheila* in the various families (Coelopidae, Dryomyzidae, Helcomyzidae) where it has been recently assigned. For these reasons the present investigation was made.

The holarctic genus now known as *Heterocheila* Rondani, 1857, has often been referred to by the synonymous name *Oedoparea* Loew, 1862. See both Steyskal (1965), and Gorodkov (1984) for complete synonymy. Included species are: (1) *H. buccata* (Fallén, 1820) (syn. *Heteromyza orientalis* Macquart, 1843), from Europe; (2) *H. hannai* (Cole, 1921) (syn. *H. nudiseta* Curran, 1933), from Pacific North America. Both species live in stranded kelp (see especially Egglshaw 1960b).

Heterocheila (or *Oedoparea*) has often been placed in the family Helcomyzidae (e. g. Malloch 1933; Hennig 1937, 1973; Steyskal, 1958, 1965; Gorodkov 1984), or in the Dryomyzidae, broadly defined to include *Helcomyza* Curtis and allied genera (e.g. Czerny 1930; Steyskal 1987; J. McAlpine 1989). Egglshaw (1960b), Dobson (1976), and Griffiths (1972) have preferred to place *Heterocheila* in the Coelopidae (with some reservations), but I have given definite reasons for its exclusion from the Coelopidae (D. McAlpine 1991), and these need not be repeated here.

Useful descriptive and illustrative material of the adult morphology of *Heterocheila* has been given by Czerny (1930), Hennig (1958), Steyskal (1958, 1962, 1987), and Griffiths (1972). Backlund (1945) and Egglshaw (1960b) have described the egg, larva and puparium of *Heterocheila*, and the latter also gives important biological information. I have examined a series of adults of both sexes of *H. buccata*, and collected the species in the field. W. N. Mathis has provided material of *H. hannai*.

The family Helcomyzidae is here considered to include only the genera *Helcomyza* Curtis, *Maoriomyia* Tonnoir & Malloch, and *Paractora* Bigot. I have given reasons for excluding the group from the Dryomyzidae (D. McAlpine 1991) and suggested a closer relationship to the Coelopidae. Useful descriptive and illustrative material of the adult morphology of Helcomyzidae has been given in most of the papers mentioned above for *Heterocheila* morphology, also by Malloch (1933). Egglshaw (1960a) has described the larva and puparium of *Helcomyza*, and given biological information. I have examined adult material of all genera and most described species of Helcomyzidae.

In the following text I use the superfamily Sciomyzoidea to include the families Sciomyzidae, Huttoninidae, Helosciomyzidae, Dryomyzidae, Helcomyzidae, Coelopidae, Ropalomeridae, Sepsidae, Chamaemyiidae (including Cremifaniidae), Eurychoromyiidae (probably excluding the *Gayomyia* complex, see J. McAlpine 1989), and Laux-

aniidae (including Celyphidae). J. McAlpine (1989) includes the last three families in a separate superfamily Lauxanioidea.

SIMILARITIES OF HETEROCHEILA TO HELCOMYZIDAE

Heterocheila shares with Helcomyzidae s. str. the beach habitat and dependence on stranded kelp, utilising it for larval nutrition as well as shelter. These habits are shared with a number of other Diptera, notably the Coelopidae, the sepsid genus *Orygma* Meigen, and the sphaerocerid genus (or subgenus) *Thoracochaeta* Duda. Similarity of habits and habitat seems to have caused some convergent similarities among these shoreline flies, so that *Orygma* and *Heterocheila* have been referred to the Coelopidae in the past.

In elevating Helcomyzidae to family status, Malloch (1933) emphasised the significance of the sclerotised precoxal bridge, which connects the prosternum to the propleuron on each side. Hennig (1958) considered this condition to represent a synapomorphy peculiar to the Helcomyzidae plus Ropalomeridae among the Schizophora, which he therefore considered to constitute a monophyletic group. It is now known that prothoracic precoxal bridges occur in at least some representatives of at least 19 schizophoran families (Speight 1969, and my observations), and many arisals of the condition are acknowledged. Within the superfamily Sciomyzoidea, the trait occurs also in some sciomyzids as an independent apomorphy. The presence of precoxal bridges is not now usually considered as proof for monophyly of Helcomyzidae and Ropalomeridae (Griffiths 1972; J. McAlpine 1989), and additional evidence is needed if monophyly of *Heterocheila* with Helcomyzidae is to be established. The precoxal bridge in *Heterocheila* differs somewhat from that of Helcomyzidae in being markedly narrower.

In both *Helcomyza* and *Heterocheila* the basal crossvein (crossvein bm-cu or base of M_{3+4} according to divergent applications of the Comstock-Needham notation) lies more obliquely, with approach to a longitudinal orientation, than in *Dryomyza*. This condition is unlikely to be a groundplan condition for Helcomyzidae s. str. in view of the fact that the undoubted helcomyzid *Maorimyza* has the basal crossvein more nearly transverse than in four available *Dryomyza* species. I also find some variation in this character in both Coelopidae and Sciomyzidae. It appears to be a rather unsatisfactory indicator of phylogenetic affinities in the Sciomyzoidea.

Heterocheila, *Maorimyza*, and *Helcomyza* have two spermathecae in the female abdomen, as dis-

tinct from the investigated dryomyzids and the apparent groundplan of Coelopidae. On the other hand the number of spermathecae is unrecorded for the helcomyzid genus *Paractora*.

Increasing knowledge of spermathecal numbers in Schizophora has demonstrated that it is a fairly unstable character. The change from three to two spermathecae must have happened many times in the evolution of the Schizophora, if, in fact, the change has always been in the one direction. In the Sciomyzoidea, variation in spermathecal number occurs within the families Huttoninidae, Coelopidae, and Sciomyzidae.

Other traits shared between *Heterocheila* and the Helcomyzidae are, so far as I am aware, found in a wide spectrum of sciomyzoid flies and have not been postulated as evidence of closer relationship between these two taxa. Such traits include the development of mollisetae (see D. McAlpine 1991) on various parts of the males, the general brownish grey pruinose covering of the cuticle, characteristic of many shore-dwelling flies, and the shining parafacial ridges, also found in many flies of maritime or sandy habitats.

DIFFERENCES BETWEEN HETEROCHEILA AND HELCOMYZIDAE

The principal morphological differences between adults of these taxa are given in table 1. They are discussed below in numerical sequence, with the addition of some comments on larval morphology (18).

1. Hackman & Väisänen (1985) have investigated the costal chaetotaxy of the Diptera (including *Heterocheila*, op. cit.: fig. 16) and assigned it some taxonomic value at the family and subfamily levels. The additional dorsal and ventral rows of costal setulae present in *Heterocheila* are in agreement with Dryomyzidae and Helosciomyzidae (but not *Coelopa frigida* (Fabricius) with which Hackman & Väisänen compare it). The absence of these series in all genera of Helcomyzidae is in contrast to the above taxa. The presence of outstanding anteroventral spines at intervals on the mid region of the costa in all Helcomyzidae separates them sharply from the Dryomyzidae and *Heterocheila*, and aligns them with Helosciomyzidae and some Coelopidae (e. g. *Lopa convexa* McAlpine, *Gluma keyzeri* McAlpine, and *Rhis whiteleyi* McAlpine, see D. McAlpine 1991).

2. The discontinuity of the parafacial suture on its lower part and peculiar angular shining parafacial ridge are apparently autapomorphies of the Helcomyzidae. The condition in *Heterocheila* is probably partly plesiomorphic, though the extensive shining ridge may be an autapomorphy.

3. The incised, vertically orientated postgenal fold in *Heterocheila*, is an unusual feature in the Sciomyzoidea and presumably an autapomorphy. A similar condition occurs in the heleomyzid *Nephelium dendrophilum* (Malloch) (D. McAlpine 1985: Fig. 30).

4. The Helcomyzidae share with the Helosciomyzidae the narrow median emargination of the face adapted to receive the prelabrum. The emargination is absent in *Heterocheila* and Dryomyzidae, but a somewhat similar emargination occurs in some, Coelopidae, though it is doubtful if it is in the groundplan of the latter. Perhaps the median emargination represents a separate apomorphy in each group in which it occurs.

5. The shape of the hypopleural channel in the Helcomyzidae represents a distinctive autapomorphy, absent in *Heterocheila* (D. McAlpine 1991: Fig. 9).

6. The significance of this character has been discussed above under 'Similarities'.

7. The male-restricted apical ventral process of the fore basitarsus is a trait difficult to evaluate phylogenetically, possibly because of irregular loss in a number of lineages (D. McAlpine 1991). In the Sciomyzoidea it is apparently restricted to Helcomyzidae, Coelopidae, and Dryomyzidae, though not uniformly present in the last family. It does not appear to be a synapomorphy as it also occurs in a number of Heleomyzoidea and in *Heloclusia imperfecta* Malloch, a somewhat primitive representative of the Neriioidea. This condition seems unlikely to have originated more than once. I therefore regard it as a very ancient trait and it may provide evidence for relationship between Sciomyzoidea, Heleomyzoidea, and Neriioidea. In this case, its absence in *Heterocheila* would be a derived state, but not necessarily a synapomorphy with other sciomyzoids in which it is also absent.

8. The phylogenetic significance of the reduction of tergite 6 of the male abdomen in Sciomyzoidea does not appear to have been satisfactorily explained. J. McAlpine (1989) regards reduction of tergite 6 as a groundplan apomorphy of his Sciomyzoidea (as distinct from Lauxanioidea) but includes in Sciomyzoidea such taxa as *Heterocheila*, *Orygma* Meigen (Sepsidae), and *Rhytidops* Lindner (Ropalomeridae) which have a large (and in *Orygma*, according to J. McAlpine, primarily unreduced) tergite 6. For this and other reasons, I include the lauxanioid families Chamaemyiidae, Lauxaniidae, and Eurychoromyiidae in the Sciomyzoidea.

If evolutionary change in the size of tergite 6 takes place only in the direction of reduction, this might seem to support the idea of a monophyletic group including Dryomyzidae, Helcomyzidae, Coe-

lopidae, and perhaps other families, but excluding *Heterocheila*, Ropalomeridae, Sepsidae, Chamaemyiidae, Lauxaniidae and Eurychoromyiidae. Convergence in this character cannot be excluded, but seems less likely for the complex Dryomyzidae plus Helcomyzidae plus Coelopidae, plus perhaps Helosciomyzidae, as these families show several other somewhat inconsistent similarities. Thus, the size of tergite 6 in *Heterocheila* makes difficulties for the hypothesis that it is close to the Helcomyzidae or Coelopidae.

9. The aedeagus of Helcomyzidae is more similar to that of Dryomyzidae than to that of *Heterocheila* (Griffiths 1972). My study of the aedeagus in Coelopidae (D. McAlpine 1991) and Heleomyzidae (e. g. D. McAlpine 1967) shows that its structure may be quite unstable above the species level.

There are apparently consistent differences in both hypandrium and aedeagus between *Heterocheila* and Helcomyzidae. The hypandrium of *Heterocheila* has two pairs of processes posteriorly (gonites or parameres) which are absent in helcomyzids. The aedeagus of *Heterocheila* has a pair of spreading lateral lobes at the junction of the basiphallus and distiphallus, which is absent in the helcomyzids examined, but it lacks the patch of pubescence near the middle of the length of the distiphallus, which is present in helcomyzids.

Griffiths (1972) has emphasised the substantial differences in external male genitalia between *Heterocheila* and certain helcomyzids. It is possible that these structures should be assigned relatively low reliability as indicators of relationship. To judge from my studies of the Heleomyzidae (D. McAlpine 1967, 1985) and the Coelopidae, the copulatory structures are so unstable above species level that it is difficult to homologue the various processes and lobes across the family. Therefore there is little logic in inferring autapomorphies between special conditions of certain coelopids and those occurring in *Heterocheila*, which is certainly not so close as a sister group to the Coelopidae. However, I find greater consistency in hypandrial structure within the smaller taxonomic diversity of the Helcomyzidae.

10. The presence of a female-restricted enlarged, isolated, posteriorly directed bristle on each lateral margin of tergites 2 to 4 and sometimes 5 is characteristic for most helcomyzids, including species in all 3 genera. It is absent in the Dryomyzidae, but the presence of similar female-restricted bristles in two rather plesiomorphic but not closely related coelopid species (D. McAlpine 1991) may indicate that it was present in the common ancestor of Helcomyzidae and Coelopidae.

11-17. I do not rate these differences in chaetotaxy very highly, taken individually. Collectively,

Table 1. Differences between Helcomyzidae and *Heterocheila* (adults).

Helcomyzidae	<i>Heterocheila</i>
1. Mid region of costa with spaced anteroventral spines, without continuous series of dorsal and ventral setulae.	Mid region of costa without anteroventral spines, with regular series of dorsal and ventral (as distinct from anterodorsal and anteroventral) setulae.
2. Shining parafacial ridge not continued posteriorly below cheek; parafacial suture obsolete or interrupted behind angular section of ridge.	Shining parafacial ridge and associated suture continued below cheek to postgenal region.
3. Postgenal fold absent.	Postgenal fold distinctly incised.
4. Epistomal margin of face with narrow sinuation to receive prelabrum.	Epistomal margin of face without narrow sinuation.
5. Hypopleural channel rather narrow and parallel-sided.	Hypopleural channel expanding rapidly anteriorly.
6. Prothoracic precoxal bridge broad, well sclerotised.	Prothoracic precoxal bridge narrow, not uniformly sclerotised.
7. ♂ fore basitarsus with terminal ventral thumbnail-like process.	♂ (and ♀) fore basitarsus without terminal ventral process.
8. ♂ abdominal tergite 6 much reduced.	♂ abdominal tergite 6 large.
9. Aedeagus with densely pubescent zone or zones, without lateral lobes.	Aedeagus without dense pubescence, with pair of lateral lobes.
10. ♀ with one large bristle near each lateral margin on tergites 2-4.	♀ (and ♂) without lateral marginal bristles on abdominal tergites.
11. Generally only 2 well developed fronto-orbital bristles present.	Fronto-orbital bristles 3.
12. Prostigmatal bristle present (sometimes replaced by several long hairs).	Prostigmatal bristle absent.
13. Median series of acrostichal bristles or setulae not differentiated.	Single regular median series of short acrostichal bristles present (in addition to prescutellar pair).
14. Prosternum setulose.	Prosternum bare.
15. Metasternum setulose.	Metasternum bare.
16. Abdominal sternite 1 setulose.	Abdominal sternite 1 bare.
17. ♀ hind tibia with subapical anterior bristle.	♀ (and ♂) hind tibia without subapical anterior bristle

the seven points indicate a notable degree of divergence between the taxa.

18. Larval morphology of Helcomyzidae is only recorded for *Helcomyza ustulata* Curtis, and it is uncertain if this is representative of the family as a whole. However, in view of the apparently close relationship between the three helcomyzid genera and the very distinctive features of the known larva, these may have some significance for higher classification. According to Egglshaw (1960a, 1960b) the third instar larva of *Heterocheila bucata* has creeping welts of small spines ventrally on

segments 3 or 4 to 12 (no such spinose creeping welts present in *Helcomyza ustulata*, but the cuticle extensively covered with backwardly directed plates), no spine above posterior spiracle (a large spine in this position in *Helcomyza*), each posterior spiracle with two or three groups of short hydrofuge hairs (these absent in *Helcomyza*). There is also difference in the arrangement and spinose armature of the ridges or processes surrounding the anus, and the position of the anus. Egglshaw considers the larvae of *Heterocheila* and *Helcomyza* to be so different that they cannot be-

long in the same family. I am unable to find in his descriptions and figures any shared distinctive traits, which might provide evidence of relatively close relationship between them, though they share many points of resemblance to numerous other schizophoran larvae.

DISCUSSION AND CONCLUSION

The few distinctive points of similarity shared between *Heterocheila* and the family Helcomyzidae are unconvincing as indicators of close phylogenetic relationship. Each of these traits occurs elsewhere in the Sciomyzoidea, and the combination or maritime habitat, a shining section of the parafacial ridge, sclerotised precoxal bridges, and two spermathecae occurs also in the genus *Tethina* Haliday (Chloropoidea: Tethinidae) though this must be only remotely related to Helcomyzidae. It must be acknowledged that convergence between *Heterocheila* and Helcomyzidae in these characters is not an improbable event.

I have indicated a possible sister-group relationship between Coelopidae and Helcomyzidae (D. McAlpine 1991) and this relationship seems to be further supported by costal chaetotaxy. The numerous character differences separating *Heterocheila* and Helcomyzidae indicate a marked evolutionary divergence, and characters 1, 6, 7, 9 and 17 in Table 1 may indicate that *Heterocheila* is probably not to be included in the monophyletic group Helcomyzidae plus Coelopidae, or even the somewhat less surely founded group Dryomyzidae plus Helcomyzidae plus Coelopidae.

Heterocheila resembles at least some taxa of the Ropalomeridae in its sclerotised prothoracic precoxal bridge, large male tergite 6, and two spermathecae. These traits, however, do not provide a stronger case for relationship than those formerly seen to support the now discarded hypothesis of close relationship between Helcomyzidae and Ropalomeridae. *Heterocheila* differs from the Ropalomeridae inter alia in its less markedly divergent postvertical bristles, differently shaped head capsule, unmodified scutellum, absence of setulae on margin of metathoracic spiracle, unmodified femora, and distinct but desclerotised distal section of vein 7. Also *Heterocheila* lives on north-temperate shore-lines, while the ropalomerids are mainly inhabitants of tropical forests of the Americas. Most recent workers (e.g. J. McAlpine 1989) consider the Ropalomeridae to be closely related to the Sepsidae. There is no adequate reason for including *Heterocheila* in this alliance.

Heterocheila also resembles the little known neotropical family Eurychoromyiidae in the prothoracic precoxal bridge, and the latter has an even

larger male tergite 6 (see J. McAlpine 1968, for morphological details). *Heterocheila* lacks the following distinctive characters of Eurychoromyiidae: body form remarkably stout; chaetotaxy greatly reduced; head structure highly modified; antennal segment 1 (scape) elongate; scutellum abbreviated; mesopleural bristles present; tibiae lacking terminal spurs; distal section of vein 7 indistinguishable. There is also considerable difference in the male postabdomens and in other characters. Whereas *Heterocheila* is restricted to cool temperate shores, eurychoromyiids are only known from Bolivia, a land-locked tropical country. I conclude that the few points of resemblance between these taxa are not indicative of close relationship.

Heterocheila is excluded from the Sciomyzidae (perhaps including Phaeomyiinae) because of the prelabrum, and its larvae feed on neither molluscs nor diplopods. Otherwise there are no special points of resemblance and no recent author has suggested a close relationship.

Heterocheila is excluded from the Huttoninidae (best regarded as a separate family, not a subfamily of Sciomyzidae or Helosciomyzidae; further discussed in the forthcoming 2nd edition of 'The Insects of Australia') because it lacks the following distinctive features of Huttoninidae: antennal segment 1 without setulae on medial surface; vein 6 abbreviated; distal section of vein 7 scarcely distinguishable; abdominal sternite 1 vestigial or absent; abdominal tergites 1 and 2 not partly separated by a membranous dorsal line. Huttoninids appear to be mainly forest-living and are endemic to New Zealand.

Heterocheila is excluded from the Helosciomyzidae because it lacks the following apparently consistent features of that family: costa with prominent spaced anteroventral spines; fronto-orbital plate with at most two bristles; prothoracic precoxal bridge absent; abdominal sternite 1 vestigial; abdominal tergite 6 of male much reduced; each posterior spiracle of larva with 4 branched hydrofuge hairs (*Helosciomyza* Hendel and *Polytocus* Lamb). Helosciomyzids are apparently restricted to the south-temperate zone. In my experience they are found in forests, grasslands, swamp-margins, and rocky shores, but are not known to inhabit kelp beds.

Heterocheila differs from the families Chamaemyiidae (including Cremifaniidae) and Lauxaniidae (including Celyphidae) in its complete vein 6 and numerous other traits. These families are morphologically more remote from *Heterocheila* than are most other sciomyzoids (J. McAlpine 1989), they are not associated with kelp, and further comparison is deemed unnecessary.

The exclusion of *Heterocheila* from all recog-

nised families of Sciomyzoidea necessitates the setting up of a new monogeneric family of this superfamily.

Heterocheilidae fam. n.

Type genus: *Heterocheila* Rondani, 1857: 104 (present designation).

Diagnostic description

Actively flying insects of maritime environments; habitus and many structural details typical of Sciomyzoidea; cuticle largely pruinose and non-shining; parts of thorax, legs, and abdomen with mollisetae, particularly developed in male.

Head. – rounded anteriorly; face somewhat convex centrally, with shallow fovea below each antenna; parafacial ridge shining, extending, together with associated suture, below cheek to postgenal region; cheek deep, setulose; postgenal fold long, distinctly incised, located towards posterior surface of head capsule; postvertical bristles often subparallel (slightly variable in orientation); fronto-orbital bristles 3, directed outwards. Antenna, at rest, subporrect; segment 1 with setulae extending on to medial surface; segment 3 rounded-oval; arista with minute pubescence, segment 5 short, not much exerted; prelabrum moderately developed, narrowly separated from face, but not fitting into sinuation on lower margin of latter.

Thorax. – Sternopleural suture not ascending posteriorly; hypopleural channel rapidly expanding anteriorly; margin of metathoracic spiracle and sternopleuron bare; prosternum broadly triangular, with narrowly sclerotised precoxal bridges; other significant characters of chaetotaxy and vestiture as in Table 1. Each tibia with one preapical dorsal bristle; all basitarsi without terminal ventral process; last 2 tarsal segments depressed and distally expanded. Costa unbroken, extending to vein 4, beyond end of subcosta with an anterodorsal series of closely placed spinules and a regular series each of dorsal, anteroventral, and ventral setulae or hairs, without spaced anterior or anteroventral spines; vein 6 visible approximately to wing margin; vein 7 beyond alula represented by long, curved crease in membrane.

Abdomen. – Tergites 1 and 2 incompletely separated by a dorsal transverse membranous line; sternite 1 short, but rather well sclerotised, bare; 7 pairs of abdominal spiracles situated in pleural membrane. Male postabdomen: tergite 6 shorter than preceding tergites but not greatly reduced, almost symmetrical, setulose; sternites 6 and 7 placed on left side; tergites 7 and 8 absent or not definitely identifiable ('8T' of Steyskal is the sclerite generally understood to be the inverted sternite 8); surstylus articulated basally, with basal anterior expansion or secondary lobe; cerci separate; basiphallus with broadly expanded membranous posterior lobe; distiphallus with complex sclerotisation and no pubescence. Female postabdomen only moderately extensible, with all segments short; tergites and sternites 6-8, epiproct, and hypoproct all well sclerotised and setulose; cerci separate, elongate.

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Nomenclatural notes

I have examined the holotype of *Heteromyza orientalis* Macquart, 1843, in the National Museum of Natural History, Paris, and find it to be identical with *Heterocheila buccata* (Fallén, 1820) (syn. n.). The given type locality of Macquart's species, Java, is erroneous; the species is probably restricted to Europe, where it is apparently absent from warmer, southern areas.

I propose the common names half-bridge flies, for representatives of the family Heterocheilidae, and bridge flies for representatives of the family Helcomyzidae. These names refer to the development of the prothoracic precoxal bridge.

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